Dealing with time-varying recruitment and length in Hill-type muscle models

Ahmed Hamouda, Laurence Kenney, David Howard

www.elsevier.com/locate/jbiomech

PII: S0021-9290(16)30963-0
DOI: http://dx.doi.org/10.1016/j.jbiomech.2016.08.030
Reference: BM7862

To appear in: *Journal of Biomechanics*

Received date: 18 August 2015
Revised date: 3 May 2016
Accepted date: 23 August 2016

Cite this article as: Ahmed Hamouda, Laurence Kenney and David Howard Dealing with time-varying recruitment and length in Hill-type muscle models *Journal of Biomechanics,* http://dx.doi.org/10.1016/j.jbiomech.2016.08.030

Original Article

Title: Dealing with time-varying recruitment and length in Hill-type muscle models

Authors' Names: Ahmed Hamouda[1], Laurence Kenney[1] and David Howard[1]

Affiliations: [1] University of Salford, United Kingdom.

Contact Information for corresponding author:

Professor David Howard

School of Computing, Science & Engineering

University of Salford

Salford, M5 4WT

United Kingdom

Telephone: +44 (0)161 295 3584

d.howard@salford.ac.uk

Keywords: multiple-motor-units; muscle model; FES

Word count (Introduction through Discussion): 3130 words

Abstract

Hill-type muscle models are often used in muscle simulation studies and also in the design and virtual prototyping of functional electrical stimulation systems. These models have to behave in a sufficiently realistic manner when recruitment level and contractile element (CE) length change continuously. For this reason, most previous models have used instantaneous CE length in the muscle's force vs. length (F-L) relationship, but thereby neglect the instability problem on the descending limb (i.e. region of negative slope) of the F-L relationship. Ideally CE length at initial recruitment should be used but this requires a multiple-motor-unit muscle model to properly account for different motor-units having different initial lengths when recruited. None of the multiple-motor-unit models reported in the literature have used initial CE length in the muscle's F-L relationship, thereby also neglecting the descending limb instability problem. To address the problem of muscle modelling for continuously varying recruitment and length, and hence different values of initial CE length for different motor-units, a new multiple-motor-unit muscle model is presented which considers the muscle to comprise 1000 individual Hill-type virtual motor-units, which determine the total isometric force. Other parts of the model (F-V relationship and passive elements) are not dependent on the initial CE length and, therefore, they are implemented for the muscle as a whole rather than for the individual motor-units. The results demonstrate the potential errors introduced by using a single-motor-unit model and also the instantaneous CE length in the F-L relationship, both of which are common in FES control studies.

Notation

a, b, a' and b' constants defining the CE's F-V relationship

CE	contractile element
$Eff.f_{iso}$	effective isometric force produced by all recruited motor units
f_{CE}	instantaneous force produced by the contractile element
f_{iso}	isometric force produced by a single-motor-unit CE model
$f_{iso,\,j}$	isometric force produced by the j^{th} motor unit
$f_{iso,\max}$	maximum isometric force produced by a single-motor-unit model
k_{PE}	stiffness of parallel passive element (PE)
k_{SE}	stiffness of series passive element (SE)
l_{CE}	instantaneous length of the contractile element
l_{mt}	instantaneous length of muscle-tendon unit
l_o	initial length of the contractile element
$l_{o,\,j}$	initial length of the j^{th} motor unit
l_{opt}	optimum length of the motor-units (for all models)
l_{PE}	length of parallel passive element (PE)
l_{SE}	length of series passive element (SE)
l_{rest}	resting length of CE (length at zero f_{SE} and zero f_{PE})
M	number of recruited motor units

PE	parallel passive element
PW	stimulation pulse width
$PW_{\max}$	maximum stimulation pulse width
R	muscle recruitment (varies continuously between 0 and 1)
R_j	j^{th} motor-unit recruitment (either 1 or 0)
SE	series passive element
v_{CE}	instantaneous velocity of the contractile element

1. Introduction

Hill-type muscle models are often used in muscle simulation studies and also in the design and virtual prototyping of functional electrical stimulation (FES) systems. These models all incorporate some representation of the muscle's force-length (F-L) relationship which is usually assumed to be a function of the instantaneous contractile element (CE) length (Lynch and Popovic, 2008; Riener and Fuhr, 1998; Ferrarin et al, 2001; Veltink et al, 1992; Schauer et al, 2005), rather than the initial CE length when recruited.

However, as Epstein and Herzog, 1998, have pointed out, using the instantaneous CE length for simulation will lead to instability on the descending limb of the F-L curve (i.e. in the region of negative slope or stiffness). This can be explained by considering a situation where equilibrium exists between a constant externally applied force and the resisting muscle force. Any infinitesimal increase in muscle length will lead to an unstable situation where there is a runaway increase in muscle length because the muscle force reduces with increasing length.

Similarly, any infinitesimal decrease in muscle length will lead to an unstable situation where there is a runaway decrease in muscle length because the muscle force rises with decreasing length.

The reason for this apparent anomaly is that the F-L relationship is simply made up of a series of static (isometric) measurements and, as such, the apparent negative stiffness of the descending limb does not reflect the true dynamic behaviour of muscles, many of which often operate on the descending limb of the F-L curve without exhibiting unstable behaviour. Indeed, on the descending limb, when an already activated muscle fibre is further stretched, the force it exerts will increase (Rassier et al, 1999; Edman et al, 1978), which is the opposite of what would occur if instantaneous length is used in simulation.

Using initial CE length (l_o) in the F-L relationship overcomes this problem and Hill-type models then exhibit stable behaviour when operating on the descending limb. Furthermore, it seems unlikely that the physics of muscle recruitment would be different on the ascending and descending limbs of the F-L curve. Therefore, to be consistent in modelling approach, it is reasonable to assume that initial length should be used for the entire F-L curve and, hence, the consequences of this will apply at all CE lengths (i.e. on both the ascending and descending limbs of the F-L curve). Therefore, the question of whether initial or instantaneous CE length should be used in the F-L relationship is critical to the correct modelling of muscle behaviour at all CE lengths.

However, as almost all muscle models used in FES control studies treat the muscle as a single contractile element (i.e. one large motor-unit), there can only be one value for l_o, which corresponds to first recruitment. But, in both normal human movement and FES control applications, it is reasonable to assume that the recruitment level (R) and the CE length (l_{CE}) change continuously and, hence, different motor-units are recruited at different lengths.

Therefore, models that treat the muscle as a single-motor-unit and, hence, use a single value for l_o would result in an over- or under-estimation of muscle force F_m. This problem could be overcome by using a multiple-motor-unit muscle model which properly accounts for different motor-units having different initial lengths when recruited.

Whilst various multiple-motor-unit models have been reported in the literature, none of these have used initial length l_o in the F-L relationship. In some cases, the motivation has been to create more complex physiologically based models that are capable of simulating the summation of individual motor-unit twitches (Riener and Quintern, 1997; Fuglevand et al, 1993). These models are valuable for simulating muscle force generation at different activation frequencies, both tetanic and sub-tetanic, and also EMG generation. However, in the vast majority of FES applications, the stimulation frequency is constant and sufficiently high to produce tetanic contraction. Furthermore, these models are usually for isometric conditions only. Therefore, for the purposes of developing FES control schemes, these models are more complex than necessary and don't cover the dynamic conditions of interest (continuously varying recruitment and CE length).

Another reason for using multiple-motor-unit models is to simulate the sequential recruitment of different muscle fibre types (Brown and Loeb, 1999, 2000a, 2000b; Brown et al, 1999; Cheng et al, 2000; Hawkins and Hull, 1992; Xia and Frey Law, 2008; Liu et al, 2002; Tang et al, 2005; Biewener et al, 2014; Wakeling et al, 2012) including their different fatigue properties, which is of greater relevance to FES control. This was one of the motivations behind the work of Brown and colleagues, which led to their Virtual Muscle modelling package (Cheng et al, 2000). Although described in different manners, in most of these models each fibre type is effectively modelled as a single motor-unit. Again, this means that there can only be one value for l_o for a particular fibre type, which corresponds to first

recruitment of that fibre type. These models all avoid this problem by using the instantaneous CE length, which leads to instability on the descending limb of the F-L curve.

In summary, none of the multiple-motor-unit models reported in the literature have used initial length l_o in the F-L relationship, thereby neglecting the descending limb instability problem. Therefore, this paper addresses the problem of muscle modelling for continuously varying R and l_{CE}, and hence different values of l_o for different motor-units. A new multiple-motor-unit model is developed which considers the muscle to comprise a large number (1000) of individual Hill-type virtual motor-units. As the recruitment level (R) varies, these virtual motor-units are recruited at different times and each with its own initial length ($l_{o,j}$ for j=1 to 1000); thus overcoming the problem described above. It should be noted that the virtual motor-units in the model don't correspond to real motor-units. Rather, the number of virtual motor-units used in the model is chosen to give the required force resolution.

Together with alternative models, the new model presented here has been used to demonstrate the scale of the potential errors involved in:

- Using instantaneous CE length instead of initial CE length in the F-L relationship.
- Treating the muscle as a single contractile element with just one initial CE length.

2. Methods

2.1 The multiple-motor-unit model

In the Hill-type single-motor-unit model described by Epstein and Herzog, 1998, it was assumed that the muscle remembers the initial CE length (l_0) at which it was first recruited

for as long as it remains recruited (i.e. for as long as $R > 0$). This is acceptable if the recruitment remains constant, but it is not accurate if R and l_{CE} are changing with time because different motor-units are then recruited at different lengths. To take this into account, we have replaced the isometric force $f_{iso}(l_o)$ used in the single-motor-unit model by an effective isometric force $Eff.f_{iso}$, which is based on the multiple-motor-unit principle (*Figure 1*). For *j*=1 to 1000, the j^{th} motor-unit remembers the length $l_{o,j}$ at which it was initially recruited and has an associated isometric force $f_{iso,j}$.

The recruitment model determines the number of recruited motor-units $M = 1000 \times R$, where R varies between 0 and 1, and M is rounded to the nearest integer. In FES applications, the input to the recruitment model is typically the pulse width (i.e. $R = PW / PW_{\max}$). Referring to *Figure 2*, the inputs to each motor-unit model are the binary recruitment (R_j) and the instantaneous *CE* length (l_{CE}), where R_j can only be 0 or 1 (de-recruited or recruited). When R_j changes from 0 to 1, the j^{th} motor-unit is recruited and a new value of $f_{iso,j}$ is calculated (from the F-L relationship) for the CE length at that particular time, and this is stored in the j^{th} motor-unit's memory. When R_j changes from 1 to 0, the j^{th} motor-unit is de-recruited and its memory erased ($f_{iso,j} = 0$).

By dividing by 1000 and using $l_{o,j}$ instead of l_o, the normalised parabolic F-L curve used by Epstein and Herzog, 1998, was adapted to calculate the isometric force exerted by a single virtual motor-unit as follows:

$$f_{iso,j} = \frac{f_{iso,\max}}{1000}[-2.777(l_{o,j}/l_{opt})^2 + 5.554(l_{o,j}/l_{opt}) - 1.777] \quad \textbf{[1]}$$

where: $l_{o,j}$ is the CE length at the time of initial recruitment of the j^{th} motor-unit; l_{opt} is the optimum CE length; and $f_{iso,\max}$ is the muscle's maximum isometric force which occurs at l_{opt}. This relationship produces the curve shown in *Figure 3* (but multiplied by 1000 in the figure). Negative values are not allowed and, to implement this, appropriate logical conditions are included to set $f_{iso,j}$ to zero.

Finally, the effective isometric force of the whole muscle is the sum of the individual forces $f_{iso,j}$ produced by all recruited motor-units.

$$Eff \cdot f_{iso} = \sum_{j=1}^{M} f_{iso,j} \qquad \textbf{[2]}$$

As mentioned above, $Eff \cdot f_{iso}$ replaces $f_{iso}(l_o)$ in the Hill-type model described by Epstein and Herzog, 1998. The remaining components of this model (F-V relationship and passive elements) are not dependent on the initial CE length and, therefore, they are implemented for the muscle as a whole rather than for the individual motor-units. *Figure 4* shows the structure of the overall model and, with the exception of the $Eff \cdot f_{iso}$ calculation described above, its implementation is similar to that described by Epstein and Herzog, 1998. The two passive elements, in parallel to and in series with the contractile element, are modelled as simple linear springs. The F-V relationship is as follows and produces the curve shown in *Figure 5*.

$$f_{CE}(v_{CE}) = \begin{cases} 0 \quad for \quad v_{CE} \le -Eff \cdot f_{iso}\dfrac{b}{a} \\ \dfrac{Eff \cdot f_{iso} b + a v_{CE}}{-v_{CE} + b} \quad for \quad -Eff \cdot f_{iso}\dfrac{b}{a} < v_{CE} \le 0 \\ 1.5Eff \cdot f_{iso} - 0.5\dfrac{Eff \cdot f_{iso} b' + a' v_{CE}}{v_{CE} + b'} \quad for \quad 0 < v_{CE} \le Eff \cdot f_{iso}\dfrac{b'}{a'} \\ 1.5Eff \cdot f_{iso} \quad for \quad v_{CE} > Eff \cdot f_{iso}\dfrac{b'}{a'} \end{cases} \qquad \textbf{[3]}$$

Where f_{CE} is the instantaneous force produced by the contractile element CE and a, b, a' and b' are constants.

2.2 Simulation study

MATLAB codes were developed for simulating the responses to open-loop stimulation protocols of two muscle models:

- The single-motor-unit model;
- The $Eff.f_{iso}$ multiple-motor-unit model.

Additionally, in both cases, the CE length used in the F-L relationship can be either the instantaneous length or the length at initial recruitment.

In order to demonstrate the need to use a multiple-motor-unit modelling approach when R and l_{CE} vary with time, input protocols are required that involve both R and l_{CE} changing over time. Two suitable protocols that have previously been used by Epstein and Herzog, 1998, were chosen as this allowed comparison with their simulation results for validation purposes (single-motor-unit model only). Details of the two protocols are as follows:

Protocol-I (*Figure 6*):

(i) 100% isometric recruitment at unique resting state (i.e. at $l_{CE} = l_{rest}$, $\Delta l_{mt} = 0$);

(ii) Stretch of 10 mm at a rate of 10mm/sec;

(iii) De-recruitment to 50%;

(iv) Shortening to $\Delta l_{mt} = 0$ at a rate of 10mm/sec;

(v) Re-recruitment to 100%.

Protocol-II (*Figure 7*):

(i) 50% isometric recruitment at unique resting state (i.e. at $l_{CE} = l_{rest}$, $\Delta l_{mt} = 0$);

(ii) Stretch of 10 mm at a rate of 10mm/sec;

(iii) Increase recruitment to 100%;

(iv) Shortening to $\Delta l_{mt} = 0$ at a rate of 10mm/sec.

The following typical values for muscle parameters, obtained from Epstein and Herzog, 1998, were used: $f_{iso,\max} = 45N$; $k_{SE} = 10\,N/mm$; $k_{PE} = 1N/mm$; $l_{rest} = 125mm$; $l_{opt} = 100\,mm$. The constants in the F-V relationship were: $a = 10\,N$; $b = 40\,mm/\sec$; $a' = 10\,N$; $b' = 30\,mm/\sec$.

When using these protocols and muscle parameters, the authors' MATLAB implementation of the single-motor-unit model produced the same force responses as those published by Epstein and Herzog, 1998.

3. Simulation Results

Simulation results are presented to compare the alternative muscle models and, in particular, to demonstrate the potential errors introduced by:

a) Treating the muscle as a single-motor-unit;

b) Using instantaneous CE length instead of CE length at initial recruitment.

3.1 Single versus multiple motor-units

Figure 8 provides a comparison of the simulation results using protocol-I for the multiple-motor-unit model versus the single-motor-unit model (both using initial CE length, l_0, in the F-L relationship). The force response for protocol-I was observed to be virtually identical over the first 5 seconds. This can be explained by considering the recruitment profile (*Figure 6*). At time zero, full recruitment occurs and the corresponding initial recruitment length is 125mm. Then recruitment drops to 50% at 3 seconds. Hence, for all active motor-units, the initial recruitment length remains the same (125mm) throughout the first 5 seconds and, therefore, both models produce the same force profile.

At 5 seconds the recruitment rises again to 100%. For the single-motor-unit model the initial CE length is still 125mm. But for the multiple-motor-unit model, the CE is already contracted and its length is therefore less than 125mm which results in a higher isometric force for the remaining 50% of motor-units. The difference is small in this protocol because the CE length is only slightly different in the two cases (overall muscle length being the same). However, it should be emphasised that the single-motor-unit model incorrectly uses the length at 0 seconds throughout.

Conversely, referring to *Figure 9*, with protocol-II and after the rise to full recruitment at 3 seconds, the multiple-motor-unit model produced a significantly different force profile. This is a direct result of the fact that the initial CE recruitment length for the motor-units recruited at 3 seconds is not the same as the length at 0 seconds which is used throughout by the single-motor-unit model. This clearly demonstrates the problem with using a single-motor-unit model when both recruitment and CE length are changing continuously as discussed earlier.

3.2 Initial CE length versus instantaneous CE length

This section compares the simulation results using the CE length at initial recruitment (l_o) as the input to the F-L relationship with those using instantaneous CE length (l_{CE}) as the input. This is done with both the single-motor-unit model and the multiple-motor-unit model.

Referring to the two recruitment protocols (*Figures 6* and *7*) and the muscle parameters given earlier, in both cases the muscle was at rest when recruitment started. Therefore the CE length at initial recruitment ($l_o = 125mm$) was used throughout the two protocols in the single-motor-unit model as this effectively consists of just one large motor-unit which is recruited immediately. Conversely the instantaneous CE length varies continuously throughout the two protocols.

During the first second after initial recruitment, the force responses for the two protocols (*Figures 10* and *11*) occur at constant musculotendon length. Nevertheless, the CE shortens and the tendon (*SE*) lengthens until the isometric CE force (at $v_{CE} = 0$) and the tendon force are equal. This shortening occurs quite quickly and the force reaches its steady state value. However, after CE shortening, the instantaneous length is different from the initial length; which explains why the force responses for the two cases are different during the first second, despite the constant length of the musculotendon complex (i.e. $\Delta l_{mt} = 0$). Similar differences in steady state forces can be observed throughout the two protocols.

When the muscle is stretching (between 1 and 2 seconds), the force increases because of the parallel element (*PE*) stiffness and also because a new equilibrium between the CE and the *SE* is established. Similarly, when the muscle shortens (between 4 and 5 seconds), the force decreases. However, the magnitudes of these changes depend on whether instantaneous or initial CE length is used in the F-L relationship because the instantaneous length changes as a new equilibrium between the CE and the *SE* is being established.

When instantaneous length is used, the results for the single-motor-unit and multiple-motor-unit models are exactly the same. This is because, in this case, there is no fundamental difference between the two models (they both use the same instantaneous length for the entire muscle at all times).

However, when using length at initial recruitment, the multiple-motor-unit results differ from those for the single-motor-unit model (*Figures 10* and *11*) because recruitment changes at different lengths (see *Figures 6* and *7*) and the multiple-motor-unit model properly accounts for this. In particular, the results diverge after recruitment rises from 50% to 100% at 5 seconds (Protocol I) and at 3 seconds (Protocol II) because the corresponding initial recruitment length for the remaining 50% of motor-units is different from that when the first 50% of motor-units were recruited at 0 seconds.

4. Conclusions

Open-loop stimulation protocols were used to compare single-motor-unit and multiple-motor-unit muscle models, using both the instantaneous CE length and the CE length at initial recruitment as the input to the F-L relationship. When instantaneous length is used as the input to the F-L relationship, the single-motor-unit model and the multiple-motor-unit model give the same results for any protocol. But, when initial recruitment length is used, both models produce results that differ significantly from those obtained using instantaneous length (as shown in Figures 10 and 11). Furthermore, when using initial length and if different motor-units are recruited at notably different lengths, the multiple-motor-unit model differs significantly from the single-motor-unit model (as shown in Figure 11). These results demonstrate the potential errors introduced by using a single-motor-unit model and also the

instantaneous CE length in the F-L relationship, both of which are common in FES control studies.

The main limitation of this work is that it is based on simulation comparisons and, therefore, can only indicate the potential errors that model assumptions may cause. To validate models such as ours, that are to be used in the design of FES systems, a comprehensive set of experimental muscle force data is required for scenarios where both recruitment and length are varying simultaneously. However, although there have been many studies on the behaviour of muscle while its length is changing; most of these were conducted at constant velocity and recruitment (e.g. Joyce et al, 1969). Where protocols include changes in recruitment, this occurs when the length is not changing (e.g. Scott et al, 1996). To the best of the authors' knowledge, experimental muscle force data is not available for protocols where muscle length and recruitment are changing simultaneously as required for our study. For this reason we adopted the same simulation protocols as Epstein and Herzog, 1998.

The multiple-motor-unit model described here could readily be extended to deal with different muscle fibre types. In this case, each fibre type would have its own set of virtual motor-units, which would be recruited at different initial recruitment lengths. The sequence of recruitment could be pre-defined in a similar way to that described in, for example, Cheng et al, 2000. Secondly, the model could also be extended to model fatigue in a more sophisticated way than has previously been done because each virtual motor-unit is recruited at a different length and time. Therefore, the fatigue of each motor-unit could properly account for both its length at initial recruitment and the time for which it has been recruited. Thirdly, where muscle geometry means that, instantaneously, different muscle fibres have different lengths, the multiple-motor-unit model could be adapted to take this into account. In this case, the muscle's length could be scaled by a factor that is specific to each motor-unit to obtain that motor-unit's length.

In summary, we suggest that the realism of muscle models can be enhanced by adopting a multiple-motor-unit modelling approach and also by using the CE length at initial recruitment (the latter to avoid instability on the descending limb of the F-L curve). Because the calculation of isometric force in the multiple-motor-unit model presented here is based on the initial length of each motor-unit when recruited, the multiple-motor-unit model properly accounts for continuously varying recruitment level and CE length, as would usually be seen in normal human movement and closed loop FES control.

Disclosure statement

To the best of the authors' knowledge, there are no conflicts of interest.

References

Biewener, A.A., Wakeling, J.M., Lee, S.S., Arnold, A.S., 2014. Validation of Hill-Type Muscle Models in relation to neuromuscular recruitment and force-velocity properties: Predicting patterns of in vivo muscle force. Integrative and Comparative Biology 54, 1072-1083.

Brown, I.E., Cheng, E.J., Loeb, G.E., 1999. Measured and modeled properties of mammalian skeletal muscle. II. The effects of stimulus frequency on force-length and force-velocity relationships. Journal of Muscle Research and Cell Motility 20, 627-643.

Brown, I.E., Loeb, G.E., 1999. Measured and modeled properties of mammalian skeletal muscle. I. The effects of post-activation potentiation on the time course and velocity dependencies of force production. Journal of Muscle Research and Cell Motility 20, 443-456.

Brown, I.E., Loeb, G.E., 2000a. Measured and modeled properties of mammalian skeletal muscle: III. the effects of stimulus frequency on stretch-induced force enhancement and shortening-induced force depression. . Journal of Muscle Research and Cell Motility 21, 21-31.

Brown, I.E., Loeb, G.E., 2000b. Measured and modeled properties of mammalian skeletal muscle: IV. dynamics of activation and deactivation. . Journal of Muscle Research and Cell Motility 21, 33-47.

Cheng, E.J., Brown, I.E., Loeb, G.E., 2000. Virtual muscle: a computational approach to understanding the effects of muscle properties on motor control. Journal of Neuroscience Methods 101, 117-130.

Edman, K.A.P., Elzinga, G., Noble, M.I.M., 1978. Enhancement of mechanical performance by stretch during tetanic contractions of vertebrate skeletal muscle fibres. Journal of Physiology 281, 139-155.

Epstein, M., Herzog, W., 1998. Theoretical models of skeletal muscle: Biological and mathematical considerations. J Wiley and Sons.

Ferrarin, M., Palazzo, F., Riener, R., Quintern, J., 2001. Model-based control of FES-induced single joint movements. IEEE Transactions on Neural Systems & Rehabilitation Engineering 9, 245-257.

Fuglevand, A.J., Winter, D.A., Patla, A.E., 1993. Models of recruitment and rate coding organization in motor-unit pools. Journal of Neurophysiology 70, 2470-2488.

Hawkins, D.A., Hull, M.L., 1992. An activation-recruitment scheme for use in muscle modeling. Journal of Biomechanics 25, 1467-1476.

Joyce, G.C., Rack, P.M., Westbury, D.R., 1969. The mechanical properties of cat soleus muscle during controlled lengthening and shortening movements. Journal of Physiology 204(2), 461-474.

Liu, J.Z., Brown, R.W., Yue, G.H., 2002. A dynamical model of muscle activation, fatigue, and recovery. Biophysical Journal 82, 2344-2359.

Lynch, C.L., Popovic, M.R., 2008. Functional electrical stimulation. IEEE Control Systems Magazine 28, 40-50.

Rassier, D.E., MacIntosh, B.R., Herzog, W., 1999. Length dependence of active force production in skeletal muscle. Journal of Applied Physiology, 86(5), 1445-1457.

Riener, R., Fuhr, T., 1998. Patient-driven control of FES-supported standing up: a simulation study. IEEE Transactions on Rehabilitation Engineering 6, 113-124.

Riener, R., Quintern, J., 1997. A physiologically based model of muscle activation verified by electrical stimulation. Bioelectrochemistry and Bioenergetics 43, 257-264.

Schauer, T., Negard, N.O., Previdi, F., Hunt, K.J., Fraser, M.H., Ferchland, E., Raisch, J., 2005. Online identification and nonlinear control of the electrically stimulated quadriceps muscle. Control Engineering Practice 13, 1207-1219.

Scott, S.H., Brown, I.E., Loeb, G.E., 1996. Mechanics of feline soleus: I. Effect of fascicle length and velocity on force output. Journal of Muscle Research and Cell Motility 17(2), 207-219.

Tang, C.Y., Stojanovic, B., Tsui, C.P., Kojic, M., 2005. Modeling of muscle fatigue using Hill's model. Bio-Medical Materials and Engineering 15, 341-348.

Veltink, P.H., Chizeck, H.J., Crago, P.E., el-Bialy, A., 1992. Nonlinear joint angle control for artificially stimulated muscle. IEEE Transactions on Biomedical Engineering 39, 368-380.

Wakeling, J.M., Lee, S.S.M., Arnold, A.S., Miara, M.D., Biewener, A.A., 2012. A Muscle's Force Depends on the Recruitment Patterns of Its Fibers. Annals of Biomedical Engineering 40, 1708-1720.

Xia, T., Frey Law, L.A., 2008. A theoretical approach for modeling peripheral muscle fatigue and recovery. Journal of Biomechanis 41, 3046-3052.

Figure captions

Figure 1: Effective isometric force model. Every recruited motor-unit is treated as a separate fully recruited *CE* for the purposes of calculating the isometric force.

Figure 2: Isometric force for a single-motor-unit. The motor-unit remembers the isometric force corresponding to its length at initial recruitment for as long as it remains recruited. On de-recruitment the memory is erased.

Figure 3: The contractile element's force-length (F-L) relationship. The normalised CE force is given by $f_{CE(normalised)} = -2.777(l_o / l_{opt})^2 + 5.554(l_o / l_{opt}) - 1.777$. The normalised CE length is given by $l_{CE(normalised)} = l_o / l_{opt}$ for a single-motor-unit model and $l_{CE(normalised)} = l_{o,j} / l_{opt}$ for an individual motor unit.

Figure 4: Structure of the Hill-type model.

Figure 5: The contractile element's force-velocity (F-V) relationship. For the multiple-motor-unit model, $Eff.f_{iso}$ replaces $f_{iso}(l_o)$.

Figure 6: Protocol-I.

Figure 7: Protocol-II.

Figure 8: Muscle force responses using protocol-I and initial CE length.

Figure 9: Muscle force responses using protocol-II and initial CE length.

Figure 10: Muscle force responses using protocol-I. Note that the two curves that result from using instantaneous length in the F-L relationship overlie each other.

Figure 11: Muscle force responses using protocol-II. Note that the two curves that result from using instantaneous length in the F-L relationship overlie each other.

Figures

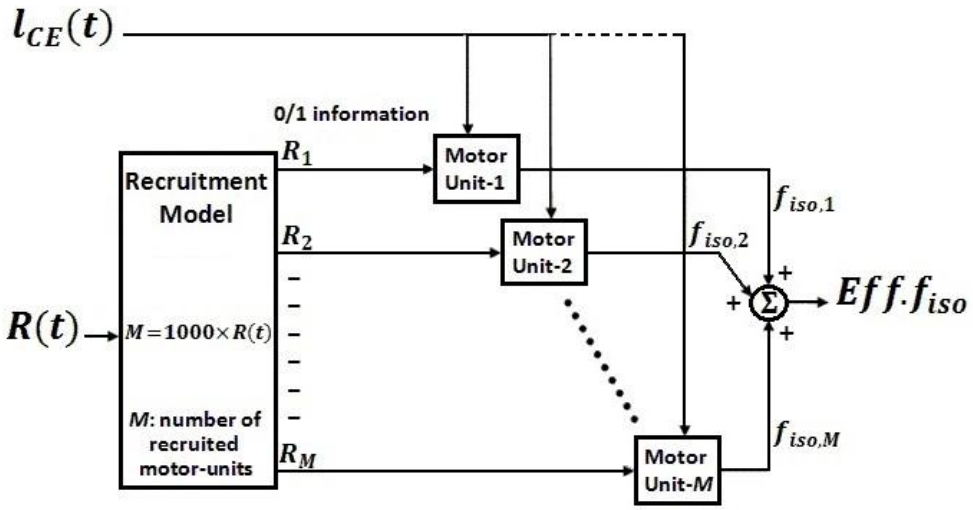

Figure 1: Effective isometric force model. Every recruited motor-unit is treated as a separate fully recruited *CE* for the purposes of calculating the isometric force.

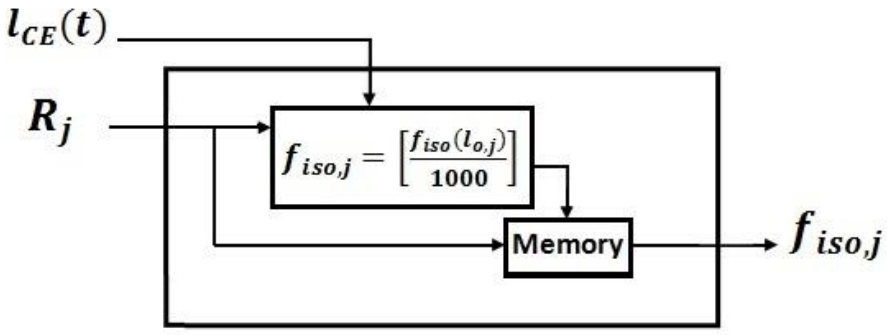

Figure 2: Isometric force for a single-motor-unit. The motor-unit remembers the isometric force corresponding to its length at initial recruitment for as long as it remains recruited. On de-recruitment the memory is erased.

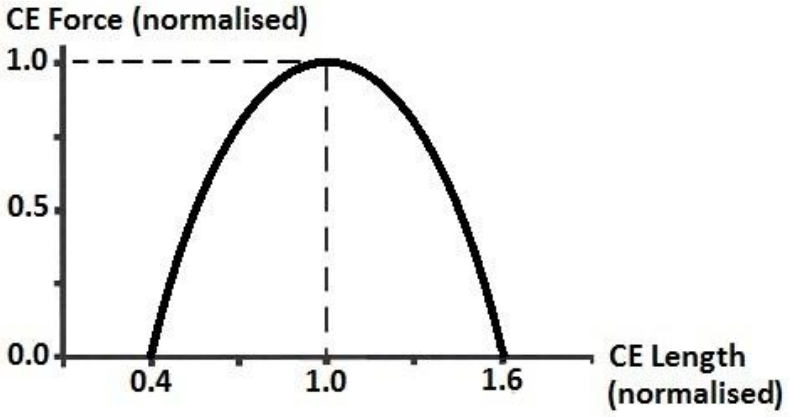

Figure 3: The contractile element's force-length (F-L) relationship. The normalised CE force is given by $f_{CE(normalised)} = -2.777(l_o / l_{opt})^2 + 5.554(l_o / l_{opt}) - 1.777$. The normalised CE length is given by $l_{CE(normalised)} = l_o / l_{opt}$ for a single-motor-unit model and $l_{CE(normalised)} = l_{o,j} / l_{opt}$ for an individual motor unit

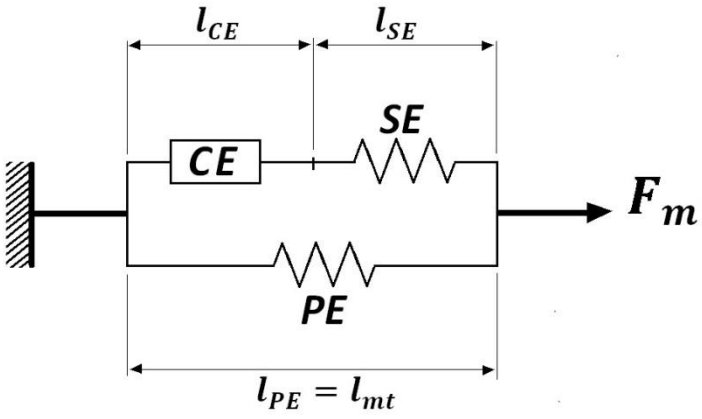

Figure 4: Structure of the Hill-type model.

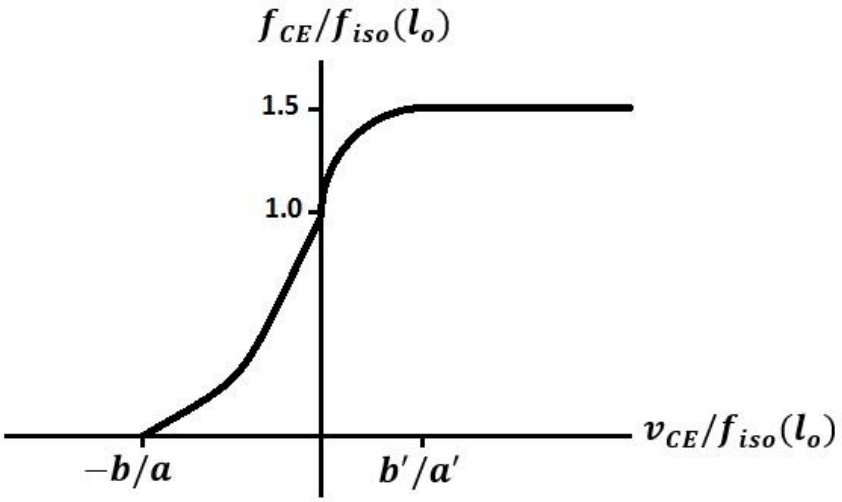

Figure 5: The contractile element's force-velocity (F-V) relationship. For the multiple-motor-unit model, $Eff.f_{iso}$ replaces $f_{iso}(l_o)$.

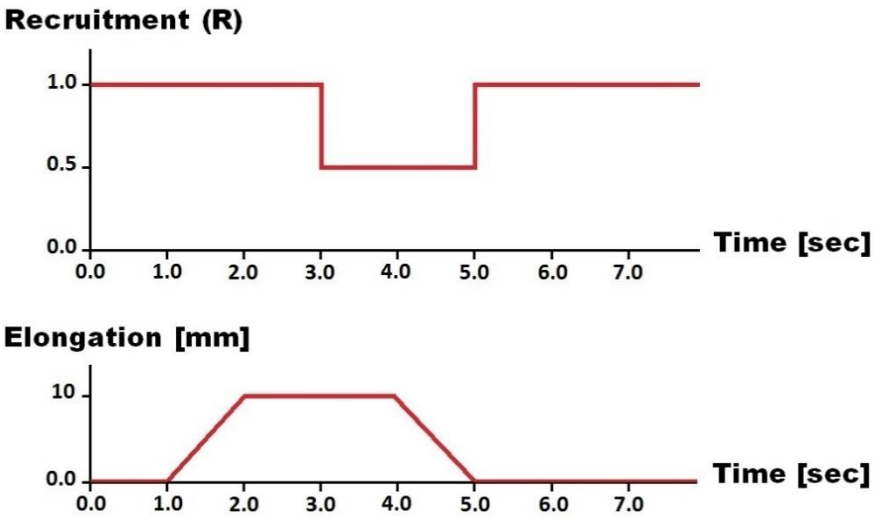

Figure 6: Protocol-I.

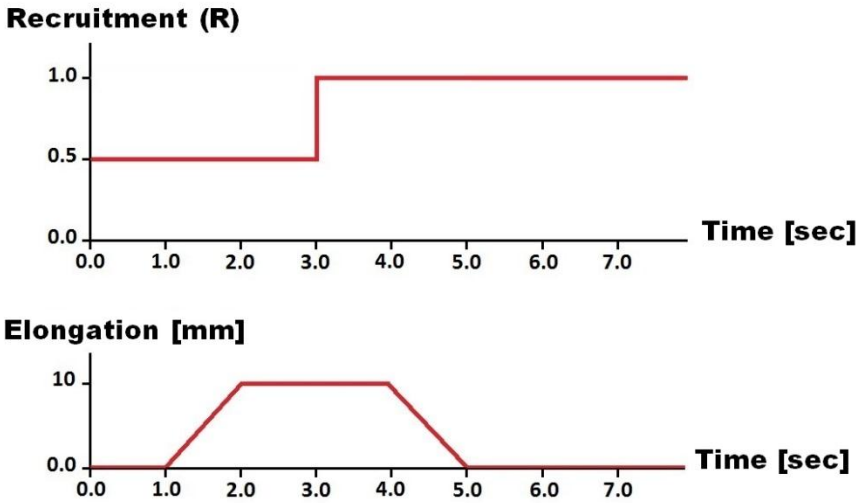

Figure 7: Protocol-II.

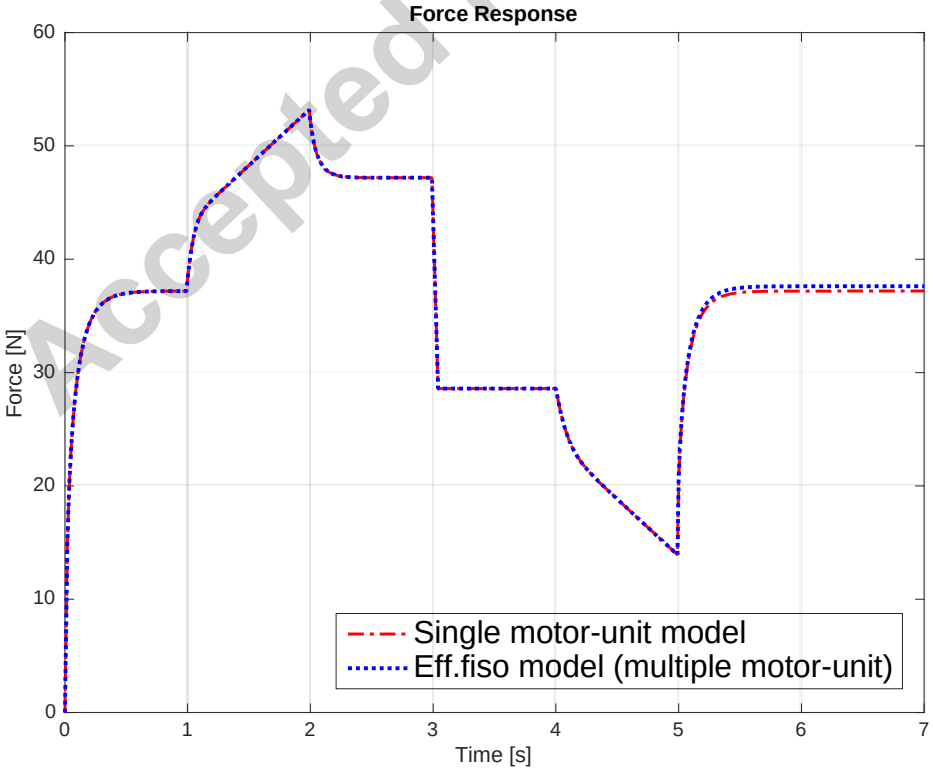

Figure 8: Muscle force responses using protocol-I and initial CE length.

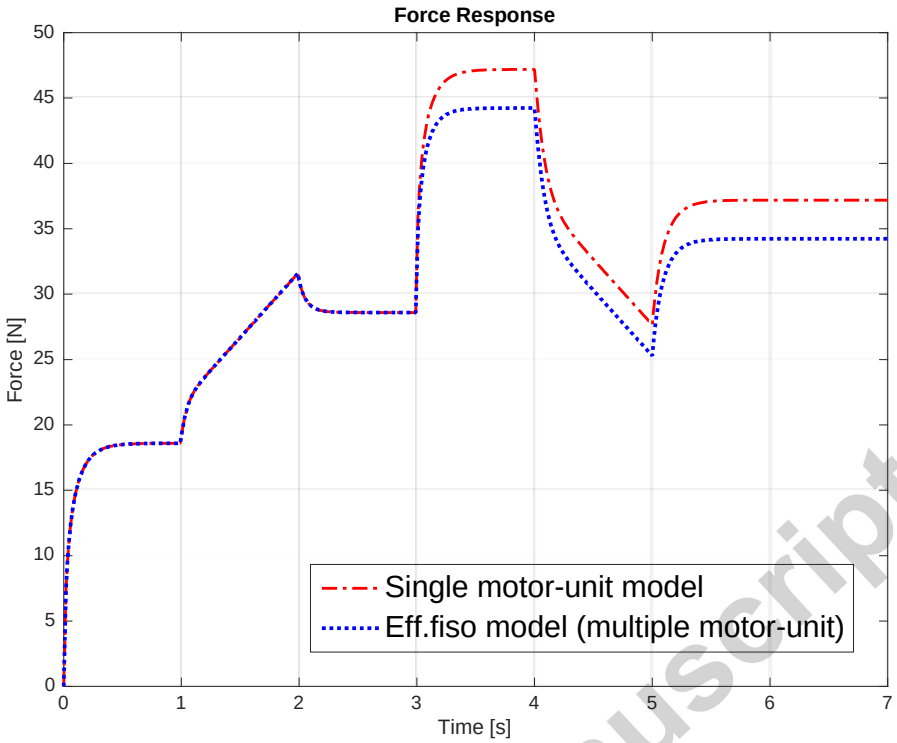

Figure 9: Muscle force responses using protocol-II and initial CE length.

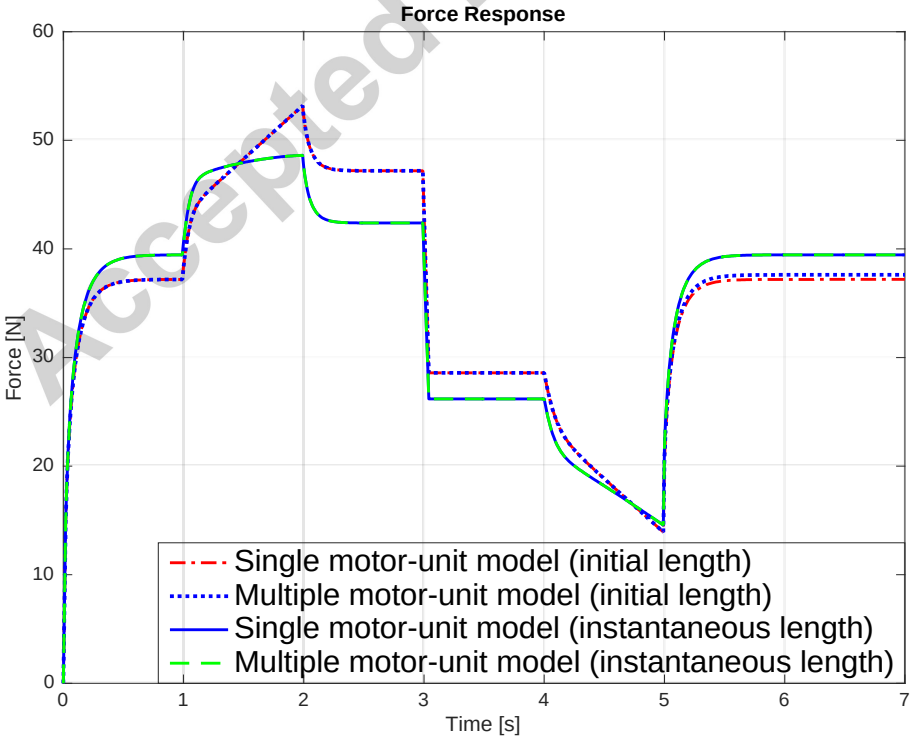

Figure 10: Muscle force responses using protocol-I. Note that the two curves that result from using instantaneous length in the F-L relationship overlie each other.

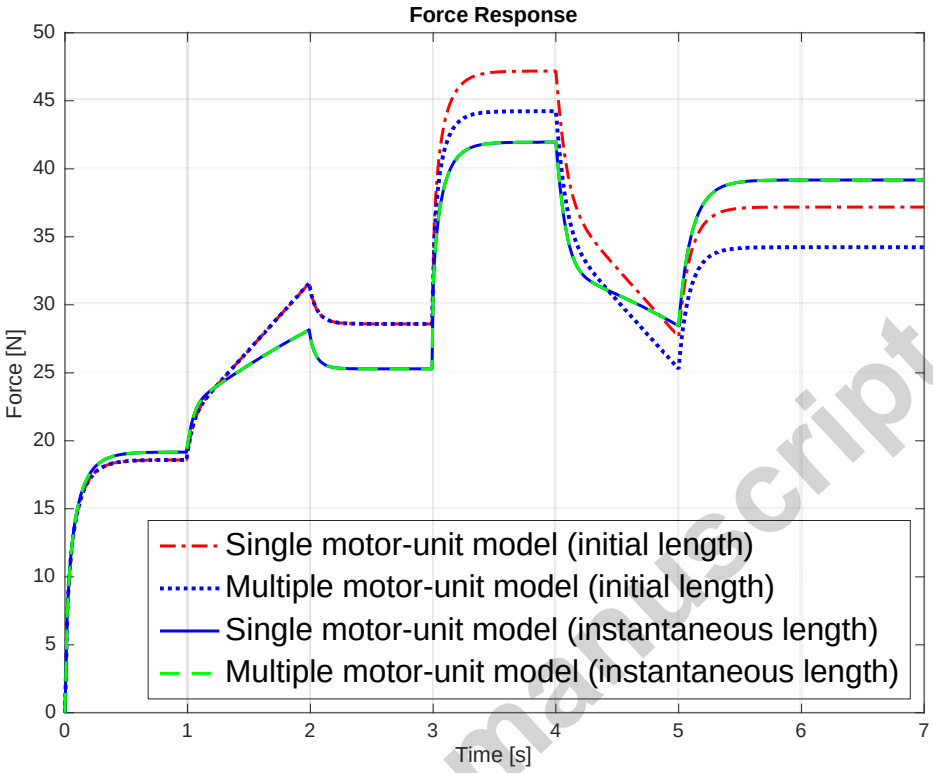

Figure 11: Muscle force responses using protocol-II. Note that the two curves that result from using instantaneous length in the F-L relationship overlie each other.